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The contributions of resource availability and social forces to foraging distributions: a spatial lag modelling approach

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The spatial distribution of foraging animals at a given time simultaneously depends on (1) exogenous environmental variables such as resource availability and abiotic habitat characteristics, and (2) the endogenous variable social aggregation made up of the opposing mechanisms of conspecific attraction and repulsion. We developed an exogenous environment–social aggregation model to analyse the spatial distributions of six abundant shorebird species in the Dutch Wadden Sea at resolutions of 150 × 150, 200 × 200 and 250 × 250 m. We used these resolutions to check the robustness of the estimates to the modifiable areal unit problem. We estimated the model parameters by spatial autoregression. This approach enables, among others, estimation of the direct and indirect effects of an exogenous environmental variable on animal density. The former is given by the regression coefficient and the latter, which is due to the amplification of the direct effect by social aggregation, by the spatial multiplier. At all resolution levels and for all species, the explanatory power of social aggregation, measured by Nagelkerke R^2, was larger than the combined contribution of the exogenous environmental variables food availability, silt content and mudflat elevation. Social aggregation was stronger for dunlin, *Calidris alpina*, red knot, *Calidris canutus*, and curlew, *Numenius arquata*, than for oystercatcher, *Haematopus ostralegus*, grey plover, *Pluvialis squatarola*, and bar-tailed godwit, *Limosa lapponica*. The total impacts (that is, direct effect plus all indirect impacts) of the exogenous environmental predictors tended to exceed substantially the direct effects (which tend to be the only ones examined in studies on foraging distributions).

Expected intake rate and predation risk are major determinants of foraging distributions (Brown & Kotler 2004; Stephens et al. 2007). Intake rate has been shown to depend negatively on interference behaviour, for example conspecific interactions such as fighting, stealing prey and monopolization of food patches (Goss-Custard 1980; Sutherland & Koene 1982; Goss-Custard et al. 2001; Vahl et al. 2005) and behaviour related to the avoidance of interactions (denoted 'cryptic interference' by Bijleveld et al. 2012). Interference sensitivity is strongly related to attack distance (Stillman et al. 2002), which depends on handling time, which in turn depends on properties of the predators and their prey (Goss-Custard 1980; Stillman et al. 2002; van Gils & Piersma 2004). In particular, interference is important when predators forage on prey items that require long handling times. Individuals may reduce the cost of interference by spacing out (Ens et al. 1990; Folmer et al. 2011; Bijleveld et al. 2012). The basic result of the conventional interference literature is that if individuals are unconstrained in selecting foraging patches, and merely suffer from the co-occurrence of conspecifics, equilibrium spatial distributions arise such that the marginal payoff among patches is equal (Fretwell & Lucas 1970; Sutherland 1983; Kacelnik et al. 1992).

Much of the conventional patch selection literature ignores the possibility that animals may also benefit from the co-occurrence of conspecifics (Brown & Orians 1970; Underwood 1982; Krause & Ruxton 2002; Nilsson et al. 2007; Campomizzi et al. 2008). Specifically, the chance of being caught by a predator decreases with group size (Hamilton 1971; Pulliam 1973). Furthermore, the presence of conspecifics provides clues about predation risks (Lima & Dill 1990) and the availability of food (e.g. Camazine et al. 2001; Valone & Templeton 2002; Danchin et al. 2004; Dall et al. 2005; Baude et al. 2008; Sumpter 2010; Deygout et al. 2010). In addition, for scrounging individuals the nearby presence of foraging conspecifics may provide foraging opportunities in that prey can be obtained by means of stealing (Giraldeau & Caraco 2000; Rutten et al. 2010). In a review of the literature, Beauchamp (1998) found that for birds, the intake rate generally increases with group size. We denote the combination of conspecific attraction and repulsion 'social aggregation' to stress the difference from

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aggregations resulting from foragers that independently from each other select the same foraging location. The benefits resulting from the presence of conspecifics are denoted 'aggregation economy' (Giraldeau & Caraco 2000). Although its relevance has been widely acknowledged in the behavioural and theoretical literature, the empirical analysis of foraging patch selection in the case of social aggregation has been hampered by the methodological problems of measuring it directly. In particular, this literature does not consider how to make predictions for field situations.

As mudflats are large and open habitats in which the benthic food stocks are buried in the sediment, the quality of foraging locations can only be assessed by trial and error or by close inspection of the mudflat surface. Therefore, shorebirds foraging on mudflats are ideal to study the effects of resource distribution and social aggregation on distributions of foragers (Piersma et al. 1993a; van de Kam et al. 2004; van Gils et al. 2006). To reduce uncertainty in the search process, shorebirds may benefit from information provided by the presence and behaviour of conspecifics (Clark & Mangel 1984; Valone 1989, 2007). The average costs and benefits of conspecific presence, however, vary from species to species. For example, red knots, *Calidris canutus*, forage on small bivalves buried in the sediment. They find bivalves by remotely sensing the sediment, which they repeatedly probe with their bills (Piersma et al. 1998). Once encountered, a prey is retrieved, handled and swallowed intact in seconds (van Gils & Piersma 2004; van de Kam et al. 2004). Because prey processing is so short, kleptoparasitism is not possible and therefore red knots are relatively insensitive to interference (Ens et al. 1990). Hence, red knots can pack together closely with minor costs (van Gils & Piersma 2004). In contrast, grey plovers, *Pluvialis squatarola*, locate their polychaete prey visually (Kersten & Piersma 1984). For instance, grey plovers can spot worms moving at the surface of the sediment over distances in the order of tens of metres. However, even when worms are abundant, the fraction that is visually detectable is usually very low (Zwarts & Wanink 1993). Hence, grey plovers are likely to detect the same prey within distances of tens of metres from each other and thus may incur interference costs. In addition, they may suffer indirectly from each other's presence because of prey depression, that is, worms decrease their surface movements so as not to be detected by predators (Charnov et al. 1976; Goss-Custard 1980; Yates et al. 2000). Hence, the presence of conspecifics decreases hunting success over relatively large distances. Thus, for grey plovers interference costs reduce conspecific attraction benefits, and therefore they maintain large interindividual distances.

Based on landscape-level field data, Folmer et al. (2010) regressed forager density on food availability and abiotic conditions (mudflat elevation, distance to high tide roost and silt content of the sediment) for six species of shorebirds. They found that the predictive power of these variables, measured by the standard deviation of the residuals, decreases with the level of flocking. For instance, for red knot the residual variance was substantially larger than for the more solitary oystercatcher, *Haematopus ostralegus*. Folmer et al. (2010) hypothesized that red knots are mainly driven by conspecific attraction and food availability, and oystercatchers mainly by food availability. Although the idea that social tendencies affect foraging behaviour is fairly straightforward, the precise way in which social aggregation should be included in a regression model specification is complex (Valcu & Kempenaers 2010). Hence, research on the impacts of resource availability and social aggregation on the spatial distribution of foraging animals has been hampered by the lack of a methodology that allows estimation of their separate effects (Beauchamp 1998; Campomizzi et al. 2008). Folmer et al. (2011) showed that social aggregation manifests itself as spatial interdependence between neighbouring foraging areas, that is, an observation (the number of foraging animals) associated with one location depends on the observations (the numbers of foraging animals) at other locations. In addition, they suggested testing the exogenous environment–social aggregation model by spatial autoregression (SAR). By means of Monte Carlo simulations, they showed that SAR performs well on gridded data. The imposition of a grid of some resolution, however, may lead to the modifiable areal unit problem (MAUP). That is, the chosen grid imposes an arbitrary measurement system on the spatial process of foraging site selection. As shown by, among others, Openshaw (1984), Fotheringham & Wong (1991), Jelinski & Wu (1996), Holt et al. (1996), Heywood et al. (1998), Fortin & Dale (2005) and Schneider (2009), MAUP can affect parameter estimates in regression analysis. However, to check the robustness of the estimates of the relationship between predictors and response variables to MAUP, Folmer et al. (2011) showed that multiscale analysis (Wiens 1989) can be applied. In addition, they showed that the direct impact of an exogenous environmental predictor such as food availability is amplified by the interdependent behaviour of the foraging animals and that SAR allows estimation of both the direct effect and the total effect (direct plus all indirect effects resulting from interdependent behaviour), the latter by means of the spatial multiplier.

Our purpose in the present study was to estimate the impacts of exogenous predictors (food and abiotic factors) and social aggregation on foraging distributions of six abundant shorebird species in the Dutch Wadden Sea at three spatial resolutions in a bid to supplement Folmer et al.'s (2010) study, which considered only the exogenous predictors. For that purpose we applied the SAR methodology developed by Folmer et al. (2011) to estimate social aggregation. To obtain further insight into the separate effects of conspecific attraction and repulsion external information is required (Folmer et al. 2011). Particularly, we made use of the information that bar-tailed godwit, *Limosa lapponica*, grey plover, oystercatcher and curlew, *Numenius arquata*, are sensitive to interference and red knot and dunlin, *Calidris alpina*, insensitive. Hence, we expected lower levels of social aggregation for the first four species than for the last two.

METHODS

Study Area

The Dutch Wadden Sea is shallow and contains large soft-sediment flats that emerge approximately twice a day. During low tide the intertidal flats are accessible to shorebirds. Intertidal flats in the Wadden Sea alternate with permanent channels. The flats are characterized by smooth gradients in terms of abiotic features, such as sediment grain size (Zwarts et al. 2004), and biological properties, such as density of macrozoobenthos (Kraan et al. 2009a). The six most abundant wader species are dunlin, red knot, oystercatcher, curlew, grey plover and bar-tailed godwit. The analysis focuses on these species because they are found in sufficiently large numbers for adequate statistical analyses and because there is large variation in flocking patterns between them.

Data Collection and Preparation

As part of a long-term benthic research programme (Piersma et al. 1993a; Kraan et al. 2009a), the density of macrozoobenthos was determined in the eastern and western Dutch Wadden Sea in July and September 2004. Benthos sampling was performed over 250 m grids in confined areas at 23 mudflats (sites). For each bird species at each sample station, we determined which prey items were available (not buried too deeply) and ingestible (smaller than maximum length and larger than minimum length; Zwarts &

Wanink 1993). For bivalves we determined the energetic value by measuring the ash-free dry mass (AFDM) in the laboratory (for details see Piersma et al. 1993b, 1995; Kraan et al. 2009b). For the specimens that were counted in the field and not brought to the laboratory (polychaetes and isopods), we obtained estimates of their energetic value from the literature (see Folmer et al. 2010 for details).

Maps of the foraging shorebirds on the 23 sites were taken from Folmer et al. (2010) and combined with maps of the distributions of species-specific harvestable benthos. Bird distributions were mapped between 2 h before and 2 h after low tide. During this period, the available habitat is at its maximum and shorebirds are able to 'space out gregariously' to reduce interference. The locations of individual birds and flocks could be determined with a precision of approximately 50 m while the benthos data were sampled on a 250 × 250 m grid. Finer resolutions than the 250 × 250 m grid of benthos biomass densities were obtained by thin plate spline interpolation. The interpolation was obtained by minimization of the residual sum of squares between the data and the predicted surface, constrained by a roughness penalty (Green & Silverman 1993; Wood 2006). The smoothing parameter is automatically chosen by generalized cross validation. Thin plate spline interpolation is simple, requires no knowledge of spatial model parameters and is suitable for positively skewed data.

For red knots, only 16 of the 23 sites observed after 1 September were included in the analysis. The reason for this was that the population of red knots in the Wadden Sea is highly variable in August because of turnover of two distinct populations. By the beginning of September the *canutus* subspecies has departed while the other subspecies, *islandica*, has taken over (Zwarts et al. 1992; Piersma et al. 1993b).

Individual birds were aggregated in grids that covered the census sites (for an example see Fig. 1). The numbers of birds inside the cells were transformed to densities (no./ha). The density of a species in each cell was related to the exogenous environmental variables, that is, density of prey (AFDM/m^2), mudflat elevation (m + NAP, the standard Dutch elevation reference) and silt content (% mass) of the sediment (obtained from Zwarts et al. 2004), and to the endogenous variable social aggregation (i.e. the density of birds in neighbouring cells). With respect to the density of prey, we included all relevant benthic species identified as food in the literature that were reasonably abundant (see Supplementary material in Folmer et al. 2010 for further information about the benthic species included). Some cells were partially outside the census site boundaries. They were included in the data set if at least 50% of the area was inside the site.

To account for the disturbance caused by the presence of the observer, cells located near the observation point were removed from the data sets. Depending on species-specific sensitivity to observer disturbance, we removed the cells whose centroids were within the following distances from the observer: dunlin and red knot: 150 m; oystercatcher, grey plover and bar-tailed godwit: 200 m; curlew: 300 m (Spaans et al. 1996). The resulting lattices contained all relevant information for statistical analysis, that is, bird and prey densities, the abiotic habitat characteristics and the geographical coordinates of each cell.

Each site was divided into cells of 250 × 250 m, 200 × 200 m and 150 × 150 m, respectively. The different resolutions were considered to check the robustness of the estimates to MAUP. The reason that we chose 250 m as the maximum cell size for analysis was to ensure a sufficient number of 'observations' for statistical analysis. The reason that we chose 150 m as the minimum cell size was related to the spatial precision of the bird mapping, which is approximately 50 m. In addition, the fraction of zeroes in the data set owing to empty cells would have increased if we had chosen a smaller cell size. The data sets consist of the aggregate of the cells over the sites. The total number of observations (which varies by cell size) for each species is given in Tables 1–6.

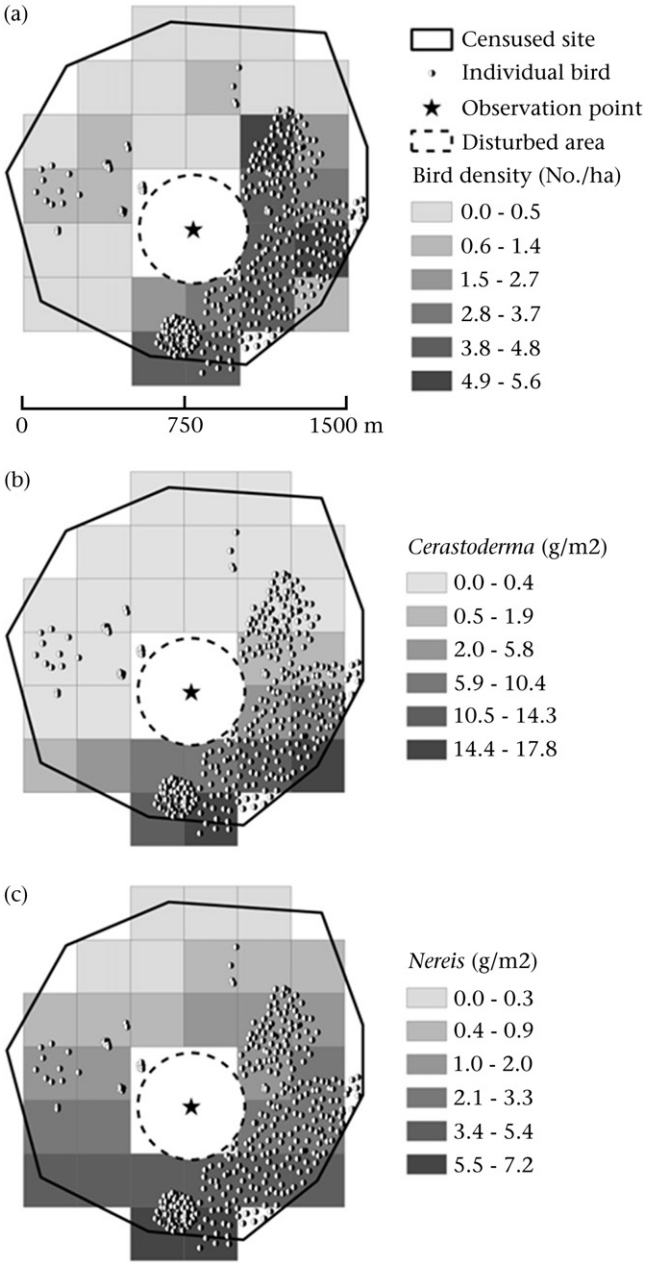

Figure 1. An example of a site with the locations of individual oystercatchers and food resources; resolution: 250 × 250 m. The dots denote individual birds. (a) Mean bird density (no./ha); (b) cockle, *Cerastoderma edule*, biomass (ash-free dry mass, g/m^2); (c) biomass of the polychaete *Nereis diversicolor* (ash-free dry mass, g/m^2). The 'hole' in the middle is the disturbed area around the observer. Cells with a centroid within the disturbed area were removed from the data set. For further details see Methods.

Statistical Analysis

The spatial lag model

We estimated the exogenous environment–social aggregation model by means of the spatial lag model which is made up of two systematic components: the spatial autoregressive component representing social aggregation and the set of exogenous variables

Table 1
Effects of exogenous variables and social aggregation ($\widehat{\rho}$) on the density of dunlins at 23 sites in the Wadden Sea at resolutions of 250 × 250 m, 200 × 200 m and 150 × 150 m

Resolution	Model	Constant	Ner	Het	Car	$\widehat{\rho}$	Wald *P*	AIC.sar	ΔAIC	AIC.lm	R^2
250	Bench	−46.22 (9.87)				0.72 (0.04)	<0.001	2036.3		2188.1	0.25
N=530	1	−52.91 (10.75)	6.25 (3.46)			0.71 (0.04)	<0.001	2035.0		2179.4	0.26
	TI		22.00 (10.88)								
	2	−40.43 (15.33)	6.01 (3.46)		2.15 (1.96)	0.71 (0.04)	<0.001	2035.8	0.8	2177.2	0.26
	TI		19.93 (12.41)		7.53 (6.82)						
	3	−43.60 (10.10)		4.89 (3.88)		0.71 (0.04)	<0.001	2036.8	1.8	2183.3	0.25
	TI			14.05 (5.79)							
200	Bench	−28.69 (6.54)				0.80 (0.03)	<0.001	3039.9		3305.2	0.27
N=851	1	−33.22 (7.19)	4.09 (2.44)			0.79 (0.03)	<0.001	3039.1		3293.1	0.27
	TI		19.85 (10.93)								
	2	−23.56 (9.90)	4.08 (2.43)		1.61 (1.19)	0.79 (0.03)	<0.001	3039.2	0.1	3286.6	0.27
	TI		18.90 (10.33)		7.88 (5.87)						
	3	−18.98 (9.47)			1.62 (1.20)	0.79 (0.03)	<0.001	3040.1	1.0	3298.5	0.27
	TI				7.64 (6.05)						
150	Bench	−12.03 (3.62)				0.89 (0.02)	<0.001	5034.8		5621.7	0.32
N=1552	1	−7.12 (5.58)	1.86 (1.13)		0.98 (0.68)	0.89 (0.02)	<0.001	5033.8		5597.5	0.32
	TI		17.36 (9.57)		9.37 (7.18)						
	2	−13.48 (3.76)	1.88 (1.13)			0.89 (0.02)	<0.001	5033.9	0.1	5605.5	0.32
	TI		17.27 (10.32)								
	3	−5.57 (5.49)			1.00 (0.68)	0.89 (0.02)	<0.001	5034.5	0.6	5613.3	0.32
	TI				9.25 (5.83)						

Bench: benchmark model, i.e. intercept and autoregressive term only (see Methods). The ecologically plausible models are ordered on the basis of Akaike's information criterion (AIC). Model 1, 2, 3: model with lowest, next lowest and third lowest AIC, respectively. *N*: number of cells; Ner: *Nereis diversicolor*; Het: *Heteromastus filiformis*; Car: *Carcinus maenas*; $\widehat{\rho}$: spatial autoregression coefficient (social aggregation); the number between parentheses for the regression coefficients: SE; the number between parentheses for the total impacts (TI): SD; Wald *P*: Wald statistic *P* value; AIC.sar: Akaike's information criterion for the model including the spatial autoregressive term; ΔAIC: difference in AIC.sar with respect to the best model; AIC.lm: AIC for the model without the spatial autoregressive term; R^2: Nagelkerke R^2; TI: the total impact of the exogenous predictor obtained by the spatial multiplier; estimate and SE of the total impact is obtained by means of Markov chain Monte Carlo simulation (see Methods).

representing the exogenous environment. The spatial lag model (Anselin 1988; Haining 2003; LeSage & Pace 2009; in matrix notation) reads:

$$Y = \rho WY + X\beta + \varepsilon$$

where Y is an $n \times 1$ vector of observations on the dependent variable (bird density), X is an $n \times k$ data matrix of explanatory variables with associated coefficient vector β, ε is an $n \times 1$ vector of error terms which follows a normal distribution, that is, $\varepsilon \sim N(0, \sigma^2 I_n)$, where I_n denotes the $n \times n$ identity matrix. W is the $n \times n$ spatial weights matrix and ρ the spatial autoregression coefficient or spatial lag parameter. The spatial weights matrix W represents spatial dependence (or connectivity) among the observations. Various types of W matrices may be employed (see Fortin & Dale 2005). We defined cells as spatially dependent if the distance between their centroids was less than or equal to 750 m. The limit of 750 m is based on the assumption that it is roughly the maximum distance over which the benefits of conspecific attraction extend. Spatial dependence was measured by inverse distance. That is, $W_{ij} = 1/d_{ij}$ if the distance between the centroids of cell i and j is less than 750 m and $W_{ij} = 0$ elsewhere. Moreover, a cell is

Table 2
Effects of exogenous variables and social aggregation ($\widehat{\rho}$) on the density of red knots at 16 sites in the Wadden Sea at resolutions of 250 × 250 m, 200 × 200 m and 150 × 150 m

Resolution	Model	Constant	Silt	Mac	Car	Mya	$\widehat{\rho}$	Wald *P*	AIC.sar	ΔAIC	AIC.lm	R^2
250	Bench	−78.67 (14.53)					0.63 (0.06)	<0.001	1348.1		1412.5	0.15
N=408	1	−65.71 (17.16)				1.91 (1.40)	0.62 (0.06)	<0.001	1348.3		1408.3	0.15
	TI					5.03 (3.40)						
	2	−74.91 (15.34)			2.77 (2.18)		0.62 (0.06)	<0.001	1348.6	0.3	1405.4	0.15
	TI				7.68 (5.77)							
	3	−95.92 (21.59)	9.52 (6.95)		3.62 (2.24)		0.60 (0.07)	<0.001	1348.7	0.4	1399.0	0.16
	TI		26.15 (17.17)		9.42 (6.00)							
200	Bench	−58.26 (10.53)					0.68 (0.05)	<0.001	1980.0		2064.2	0.12
N=652	1	−49.82 (12.19)				1.21 (0.90)	0.67 (0.05)	<0.001	1980.2		2059	0.13
	TI					3.47 (2.60)						
	2	−55.84 (11.07)			1.97 (1.50)		0.66 (0.06)	<0.001	1980.4	0.2	2054.4	0.13
	TI				6.35 (4.45)							
	3	−70.20 (15.21)	6.54 (4.82)		2.63 (1.56)		0.65 (0.06)	<0.001	1980.5	0.3	2047.4	0.13
	TI		20.39 (14.81)		7.46 (4.80)							
150	Bench	−19.60 (4.40)					0.85 (0.03)	<0.001	3155.3		3407.0	0.19
N=1203	1	−17.72 (4.55)		1.33 (0.90)			0.85 (0.03)	<0.001	3155.1		3402.6	0.19
				9.42 (6.84)								
	2	−14.10 (5.86)				0.68 (0.50)	0.85 (0.03)	<0.001	3155.4	0.3	3395.1	0.19
	TI					4.65 (3.38)						
	3	−13.49 (5.84)		1.13 (0.92)		0.56 (0.51)	0.85 (0.03)	<0.001	3155.9	0.5	3393.7	0.19
	TI			7.24 (6.38)		3.56 (3.54)						

Silt: silt content (%); Mac: *Macoma balthica*; Car: *Carcinus maenas*; Mya: *Mya arenaria*. See Table 1 for further details.

Table 3
Effects of exogenous variables and social aggregation (ρ_hat) on the density of oystercatchers at 23 sites in the Wadden Sea at resolutions of 250 × 250 m, 200 × 200 m and 150 × 150 m

Resolution	Model	Constant	Silt	Mac	Cer	Ner	$\hat{\rho}$	Wald *P*	AIC.sar	ΔAIC	AIC.lm	R^2
250	Bench	−36.77 (8.57)					0.66 (0.05)	<0.001	1894		1998.9	0.19
N=509	1	−43.18 (8.98)			4.14 (2.76)	3.51(2.30)	0.61 (0.05)	<0.001	1889.5		1970.7	0.20
	TI				11.18 (6.98)	8.78 (5.94)						
	2	−40.46 (9.02)		6.38 (4.40)		4.27 (2.13)	0.61 (0.05)	<0.001	1889.6	0.1	1969.5	0.20
	TI			17.11 (10.24)		10.35 (5.34)						
	3	−41.92 (8.91)				5.14 (2.04)	0.62 (0.05)	<0.001	1889.7	0.2	1974.5	0.20
	TI					13.96 (5.65)						
200	Bench	−23.97 (5.95)					0.74 (0.04)	<0.001	2886.7		3069.8	0.20
N=821	1	−24.60 (6.08)		4.98 (3.00)	2.85 (1.56)		0.71 (0.04)	<0.001	2881.8		3036.7	0.21
	TI			17.10 (10.49)	9.36 (5.51)							
	2	−27.45 (6.52)		4.90 (3.07)		3.42 (2.07)	0.70 (0.04)	<0.001	2882.4	0.6	3028.4	0.21
	TI			16.29 (11.12)		11.08 (7.41)						
	3	−25.52 (6.02)			3.66 (1.48)		0.72 (0.04)	<0.001	2882.5	0.7	3044.6	0.21
	TI				13.26 (5.33)							
150	Bench	−10.27 (3.35)					0.85 (0.02)	<0.001	4708.8		5121.3	0.24
N=1500	1	−10.38 (3.36)			2.38 (0.82)		0.83 (0.03)	<0.001	4702.1		5075.9	0.25
	TI				14.43 (5.10)							
	2	−9.88 (3.40)		2.09 (1.65)	2.08 (0.85)		0.83 (0.03)	<0.001	4702.5	0.4	5062.3	0.25
	TI			12.32 (10.24)	12.37 (5.01)							
	3	−13.49 (7.48)	1.51 (3.24)		2.33 (0.82)		0.83 (0.03)	<0.001	4703.9	1.8	5076.6	0.25
	TI		7.81 (18.71)		14.59 (5.63)							

Silt: silt content (%); Mac: *Macoma balthica*; Cer: *Cerastoderma edule*; Ner: *Nereis diversicolor*. See Table 1 for further details.

considered nondependent with itself, that is, $W_{ii} = 0$. W was normalized so that the spatial lag parameter is between −1 and 1. The parameter ρ reflects spatial dependence in the sample. That is, it measures the weighted impact of spatially dependent cells on observations in the vector Y caused by social aggregation.

In SAR, the regression coefficient of an exogenous environmental variable does not represent the total change in Y in response to a unit change in that variable, as in a standard linear model, because the indirect impacts from spatial autocorrelation are not taken into account. That is, an exogenous variable in a given cell attracts birds, which in turn attract other birds to their own and neighbouring cells (first-order indirect effect), which in turn attract birds to their own and neighbouring cells (second-order indirect effect) and so on (see LeSage & Pace 2009 for details). To obtain the total effect the indirect effects also need to be taken into account (Folmer et al. 2011). The total effect (direct + all indirect effects) of a given exogenous variable on animal density can be obtained by multiplying its SAR coefficient by the spatial multiplier $1/(1-\rho)$. Estimates and standard deviations of the total effects were obtained by means of Markov chain Monte Carlo simulation (Bivand et al. 2008a; LeSage & Pace 2009).

Model specification

The dependent variable is the density of birds (no./ha) in each cell of the lattice. To reduce skewness the response variable was ln transformed before estimation (Gelman & Hill 2006). The argument of the ln function was increased by half the smallest nonzero value observed to avoid arguments equal to 0.

Table 4
Effects of exogenous variables and social aggregation ($\hat{\rho}$) on the density of bar-tailed godwits at 23 sites in the Wadden Sea at resolutions of 250 × 250 m, 200 × 200 m and 150 × 150 m

Resolution	Model	Constant	Elev	Ner	Are	Lan	Het	$\hat{\rho}$	Wald *P*	AIC.sar	ΔAIC	AIC.lm	R^2
250	Bench	−76.79 (11.70)						0.67 (0.05)	<0.001	1056		1190.9	0.24
N=509	1	−78.59 (11.94)	−10.36 (7.06)					0.66 (0.05)	<0.01	1055.9		1179.3	0.24
	TI		−30.27 (23.02)										
	2	−79.36 (11.96)				1.27 (0.88)		0.66 (0.05)	<0.001	1056.0	0.1	1181.4	0.24
	TI					3.65 (2.66)							
	3	−81.10 (12.22)	−15.50 (7.93)	1.32 (0.98)				0.65 (0.05)	0.003	1056.1	0.2	1169.9	0.24
	TI		−43.54 (22.35)	3.43 (2.63)									
200	Bench	−64.69 (9.39)						0.67 (0.05)	<0.001	1225.1		1377.2	0.17
N=821	1	−68.93 (9.79)	−12.51 (4.84)	1.64 (0.80)				0.65 (0.05)	<0.001	1221.8		1355.1	0.18
	TI		−33.98 (14.47)	4.23 (2.37)									
	2	−70.52 (9.93)	−13.32 (4.89)	1.48 (0.82)	1.06 (0.96)			0.64 (0.05)	<0.001	1222.6	0.8	1349.6	0.18
	TI		−36.52 (12.51)	4.06 (2.39)	3.06 (2.91)								
	3	−68.16 (9.81)	−12.74 (4.85)	1.33 (0.90)			0.68 (0.94)	0.65 (0.05)	<0.001	1223.3	1.5	1356.4	0.18
	TI		−36.88 (12.98)	3.93 (2.53)			1.89 (2.77)						
150	Bench	−32.77 (4.99)						0.77 (0.03)	<0.001	1716.1		2028.1	0.19
N=1500	1	−34.66 (5.21)	−5.86 (2.94)	0.56 (0.35)				0.75 (0.04)	<0.001	1715.6		1989.8	0.19
	TI		−24.06 (12.85)	2.17 (1.47)									
	2	−33.43 (5.07)	−3.57 (2.60)					0.76 (0.04)	<0.001	1716.2	0.6	2010.2	0.19
	TI		−14.60 (11.16)										
	3	−33.21 (5.12)	−4.36 (2.75)				0.41 (0.48)	0.76 (0.04)	<0.001	1717.4	1.8	2007.8	0.19
	TI		−17.81 (12.95)				1.71 (2.09)						

Elev: elevation; Ner: *Nereis diversicolor*; Are: *Arenicola marina*; Lan: *Lanice conchilega*; Het: *Heteromastus filiformis*. See Table 1 for further details.

Table 5
Effects of exogenous variables and social aggregation ($\widehat{\rho}$) on the density of curlews at 23 sites in the Wadden Sea at resolutions of 250 × 250 m, 200 × 200 m and 150 × 150 m

Resolution	Model	Constant	Elev	Silt	Lan	$\widehat{\rho}$	Wald *P*	AIC.sar	ΔAIC	AIC.lm	R^2
250	Bench	−70.30 (10.84)				0.67 (0.05)	<0.001	1132.8		1250.3	0.23
N=460	1	−73.67 (11.28)	−20.03 (9.32)			0.64 (0.05)	<0.001	1130.3		1228.2	0.24
	TI		−56.96 (27.59)								
	2	−80.23 (14.77)	−23.53 (10.60)	3.22 (4.74)		0.64 (0.05)	<0.001	1131.8	1.5	1228.3	0.24
	TI		−67.56 (29.20)	9.62 (12.91)							
	3	−74.03 (11.33)	−18.71 (10.33)		0.26 (0.80)	0.64 (0.05)	<0.001	1132.2	1.9	1226.7	0.24
	TI		−49.80 (29.10)		8.36 (2.31)						
200	Bench	−41.85 (6.66)				0.76 (0.04)	<0.001	1613.7		1840.8	0.26
N=747	1	−44.16 (6.96)	−13.93 (6.16)			0.74 (0.04)	<0.001	1610.6		1803.7	0.27
	TI		−51.42 (26.29)								
	2	−44.51 (7.00)	−12.44 (6.80)		0.34 (0.62)	0.73 (0.04)	<0.001	1612.3	1.7	1799.3	0.27
	TI		−48.89 (26.72)		1.21 (2.23)						
	3	−46.58 (9.30)	−15.18 (6.93)	1.22 (3.19)		0.74 (0.04)	<0.001	1612.5	1.9	1804.8	0.27
	TI		−53.58 (24.41)	3.09 (12.75)							
150	Bench	−19.28 (3.34)				0.85 (0.02)	<0.001	2330.7		2744.3	0.26
N=1357	1	−19.79 (3.45)	−5.61 (3.68)			0.84 (0.02)	<0.001	2330.4		2700.4	0.27
	TI		−33.34 (20.75)								
	2	−19.61 (3.41)			0.35 (0.34)	0.84 (0.02)	<0.001	2331.6	1.2	2717.7	0.26
					2.28 (2.25)						
	3	−22.15 (5.10)	−6.79 (4.13)	1.18 (1.88)		0.84 (0.03)	<0.001	2332.0	1.6	2699.4	0.27
	TI		−40.71 (28.06)	7.43 (12.33)							

Elev: elevation; silt: silt content (%); Lan: *Lanice conchilega*. See Table 1 for further details.

Regarding the explanatory variables, we started the analysis with a model that included the autoregressive component, all relevant benthos species that were reasonably abundant, and the abiotic variables silt content and elevation of the mudflat (see Folmer et al. 2010). Skewness of the distributions of the food variables and nonlinear relationships between forager density and food density (van der Meer & Ens 1997) were handled by ln transformation of the food variables. Again, to avoid zero arguments, every argument was increased by half of the smallest nonzero value observed. The abiotic predictors were not transformed.

We estimated by means of SAR all models ranging from the full model with all relevant exogenous predictors and the autoregressive term included to a social aggregation model with intercept and autoregressive term only. Models with negative coefficients of prey variables were considered implausible. Since we did not have a priori expectations about the signs of silt content and elevation for any bird species, negative and positive coefficients were considered ecologically plausible.

To assess the relative importance of plausible exogenous environmental predictors and social aggregation, we compared the full model and the model with social aggregation only (i.e. the benchmark model) by means of the Nagelkerke R^2 (Nagelkerke 1991):

$$R^2 = \frac{1 - \left\{\dfrac{L(M_{\text{intercept}})}{L(M_{\text{SAR}})}\right\}^{2/n}}{1 - \left\{L(M_{\text{intercept}})\right\}^{2/n}}$$

Table 6
Effects of exogenous variables and social aggregation ($\widehat{\rho}$) on the density of birds at 23 sites in the Wadden Sea at resolutions of 250 × 250 m, 200 × 200 m and 150 × 150 m: the grey plover models

Resolution	Model	Constant	Silt	Nep	Lan	Ner	$\widehat{\rho}$	Wald *P*	AIC.sar	ΔAIC	AIC.lm	R^2
250	Bench	−105.7 (14.91)					0.56 (0.06)	<0.001	837.28		893.08	0.11
N=509	1	−126.25 (17.61)	6.55 (3.01)	2.64 (1.03)		2.56 (1.29)	0.51 (0.06)	<0.01	832.24		874.95	0.13
	TI		12.82 (6.36)	5.45 (1.99)		5.47 (2.77)						
	2	−129.28 (17.82)	7.02 (3.03)	2.26 (1.07)	0.67 (0.50)	2.75 (1.30)	0.50 (0.07)	<0.01	832.47		873.55	0.13
	TI		13.96 (6.02)	4.53 (2.27)	1.48 (1.01)	6.02 (2.66)						
	3	−121.68 (17.27)	7.19 (3.01)	2.03 (0.99)			0.53 (0.06)	<0.01	834.13		882.53	0.12
	TI		15.68 (7.04)	4.42 (2.30)								
200	Bench	−76.01 (10.63)					0.62 (0.05)	<0.001	1090.3		1172.5	0.10
N=821	1	−90.49 (12.44)	4.76 (2.01)	1.75 (0.65)		1.58 (0.87)	0.58 (0.06)	<0.001	1084.5		1149.4	0.11
	TI		11.85 (4.68)	4.12 (1.62)		3.65 (2.35)						
	2	−87.38 (12.19)	5.14 (2.00)	1.43 (0.62)			0.59 (0.05)	<0.001	1085.7		1157.4	0.11
	TI		12.50 (4.92)	3.63 (1.56)								
	3	−91.91 (12.56)	4.96 (2.03)	1.66 (0.66)	0.27 (0.38)	1.66 (0.88)	0.57 (0.06)	<0.01	1086.0		1148.9	0.11
	TI		11.79 (5.06)	4.03 (1.64)	0.65 (0.87)	3.95 (2.01)						
150	Bench	−38.99 (5.71)					0.73 (0.04)	<0.001	1208		1378.7	0.11
N=1500	1	−44.10 (6.54)	2.29 (1.14)	0.64 (0.39)			0.72 (0.04)	<0.001	1207.1		1362	0.11
	TI		8.44 (3.83)	2.50 (1.35)								
	2	−45.09 (6.64)	1.96 (1.06)		0.35 (0.21)		0.71 (0.04)	<0.001	1207.1		1359.6	0.11
	TI		6.81 (4.14)		1.27 (0.72)							
	3	−45.14 (6.62)	2.50 (1.15)	0.51 (0.40)	0.27 0.22)		0.71 (0.04)	<0.001	1207.5		1359.9	0.11
	TI		8.49 (3.75)	1.69 (1.42)	1.04 (0.82)							

Silt: silt content (%); Nep: *Nephtys hombergii*; Lan: *Lanice conchilega*; Ner: *Nereis diversicolor*. See Table 1 for further details.

where n is the number of observations, $L(M_{\text{intercept}})$ and $L(M_{\text{SAR}})$ are the log-likelihood values of models with intercept only and the two types of SAR models (type 1: intercept + spatial autoregressive component only; type 2: intercept + spatial autoregressive component + exogenous variables), respectively. Improvement in terms of variance explained between both types of models was given by the difference between both R^2s. We also estimated the Akaike's information criterion (AIC) of a model without and with the spatial autoregressive component. The best three models based on the AIC value and exogenous environmental variables with ecologically plausible signs are presented in Tables 1–6.

We used the R environment version 2.13.1 (R Development Core Team 2009) for the statistical analyses, including geographical interpolation. Specifically, the procedure of interpolation and geographical overlaying was automated by applying functions from the packages fields (Furrer et al. 2009), maptools (Lewin-Koh et al. 2008), sp (Pebesma & Bivand 2005; Bivand et al. 2008b) and spatstat (Baddeley & Turner 2005). We used the package spdep (Bivand et al. 2008a) to estimate the spatial lag model by means of maximum likelihood and to calculate the total effects of the exogenous predictors, including the associated dispersion measures (standard deviations).

RESULTS

Before turning to the estimations, we note that because of conspecific attraction, large parts of the mudflats tend to be unoccupied (Folmer et al. 2010). As noted above, the resulting skewness of the dependent variable was reduced by ln transformation. The frequency distributions of the ln-transformed response variables ($\ln(\text{no./ha} + c)$, where c is half the smallest nonzero value) also contained a peak at the left end. The frequency distributions of the residuals after SAR estimation, however, turned out to be close to normal (although a bit peaked, Fig. 2), which means that the maximum likelihood estimator is consistent and asymptotically normal.

The following patterns emerge from Tables 1–6. First, there is evidence of MAUP, since the estimated coefficients for both social aggregation and the exogenous environmental variables vary by resolution. However, the following robust patterns emerge. First, for all species for all resolutions the estimated autoregression coefficients are significant at the 5% level. This result is supported by the substantial differences in AICs between the models with and without the SAR component. Furthermore, $\widehat{\rho}$ increases with resolution, which is due to the increase in similar adjacent cells.

Second, as argued above, $\widehat{\rho}$ is the net outcome of the two opposing mechanisms conspecific attraction and repulsion. To draw conclusions about each mechanism separately, external information is required (Folmer et al. 2011). For the six species under consideration this kind of information exists. Particularly, bar-tailed godwit, grey plover, oystercatcher and curlew are known to be sensitive to interference and red knot and dunlin insensitive.

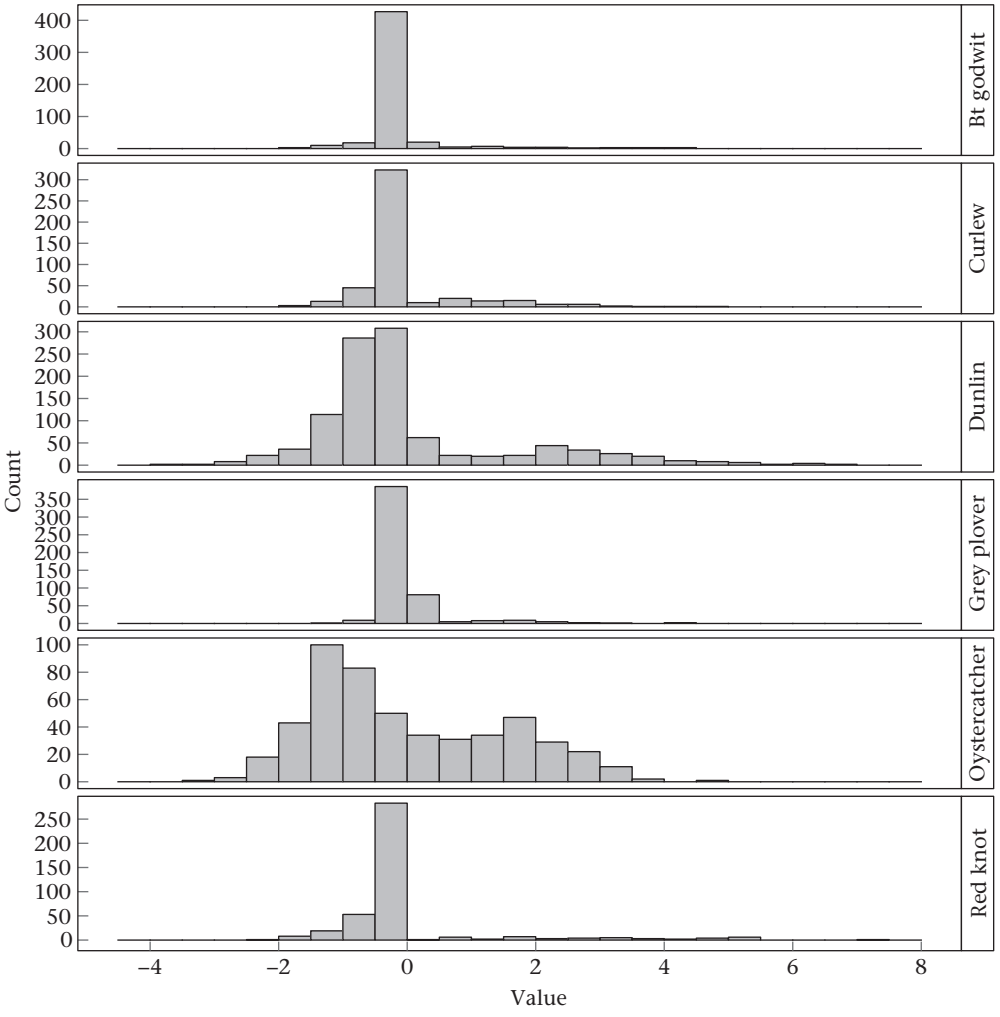

Figure 2. Histograms of the residuals of the best SAR models by shorebird species at the 250 × 250 m scale.

Hence, we expected smaller $\hat{\rho}$'s for the first four species than for the last two, especially at smaller scales. The results in Tables 1–6 are in line with this expectation (see also Fig. 3).

Third, the exogenous predictors follow a similar pattern as social aggregation in that the best, second-best and third-best models vary by resolution. However, for a given species the same environmental variables frequently show up as relevant predictors at various resolutions. In addition, for a given species for a given resolution, the best, second-best and third-best model tend to differ only slightly in terms of AIC and Nagelkerke R^2. Possible explanations for this are the low predictive power of the exogenous variables and high multicollinearity between them. This is supported by the small differences in AIC between the best and successive models (ΔAIC), suggesting that the best models are only marginally better than the second-best and third-best models. Given these findings, we accept all the food items and abiotic habitat characteristics that have been identified by the best three models as relevant predictors.

Tables 1–6 show that for dunlin the prey species *Nereis diversicolor*, *Heteromastus filiformis* and *Carcinus maenas* are the main exogenous predictors, for red knot *C. maenas*, *Mya arenaria*, *Macoma balthica* and silt content, for oystercatcher *Cerastoderma edule*, *M. balthica*, *N. diversicolor* and silt content, and for bar-tailed godwit *N. diversicolor*, *Lanice conchilega*, *Arenicola marina*, *H. filiformis* and elevation. *Lanice conchilega* is the most important food predictor for curlew. Furthermore, curlews are relatively more abundant on relatively low and silty mudflats. Finally, *Nephtys hombergii*, *L. conchilega* and *N. diversicolor* are the most important prey variables for grey plover. In addition, this species shows a preference for mudflats with relatively high silt content.

The most striking result in Tables 1–6 is that social aggregation outweighs the exogenous predictors in terms of explanatory power. Comparison of the Nagelkerke R^2 s of the models with intercepts and autoregressive component only versus the models with intercepts, autoregressive component and exogenous predictors shows that for the latter this statistic is only slightly higher than for the former for all species at all levels of resolution.

The regression coefficients of the exogenous environmental predictors represent their direct effects only. The full impact of an exogenous predictor is given by its total impact (also presented in Tables 1–6). To obtain the total effects, the coefficients of the exogenous predictors were multiplied by the spatial multiplier. The main finding is that the total effect outweighs the direct effect (represented by the regression coefficient), a result that holds for all species at all resolutions. Obviously, the larger the coefficient of an exogenous predictor and the larger the degree of social aggregation, the larger is the total impact. For instance, for dunlins the spatial autocorrelations are highest at resolution 150 × 150 m. Hence, the difference between the regression coefficients of the exogenous predictors (direct impacts) and the corresponding total impacts are largest for this resolution.

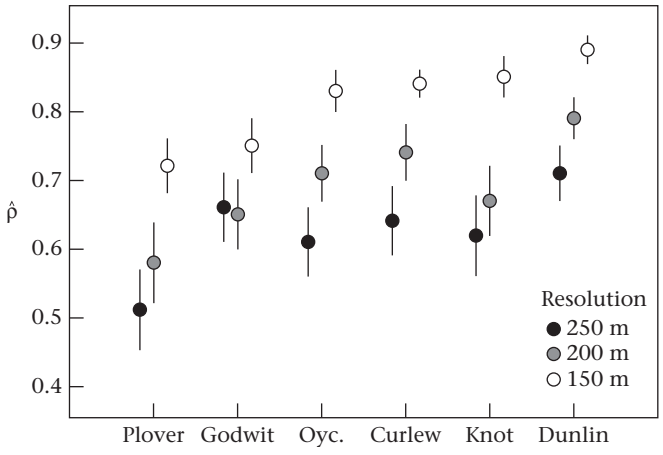

Figure 3. Spatial dependence ($\hat{\rho}$) by resolution and shorebird species in the Dutch Wadden Sea. Oyc = oystercatcher.

DISCUSSION

Ignoring social aggregation as an explanatory variable in empirical analysis of foraging behaviour is likely to lead to misleading results. Particularly, in regression analysis the estimators of the regression coefficients of the variables included in the model and their variances are biased if social aggregation is omitted as an explanatory variable (Legendre 1993; Keitt et al. 2002; Lichstein et al. 2002; Beale et al. 2010). In this paper we have operationalized social aggregation as spatial dependence and applied spatial autoregression to estimate the full exogenous environment–social aggregation model to overcome bias from omitted variables.

The results presented above substantiate the importance of social aggregation. Indeed, we have found that for all the species, at all three levels of resolution, social aggregation outweighs the exogenous predictors in terms of explanatory power. These results substantiate the notion that the group represents a central component of the environment for different species of foraging shorebirds. However, the small differences in explanatory power between the models with constant and autoregressive component on the one hand and the full models with constant, autoregressive component and exogenous predictors on the other do not imply that the exogenous predictors play a negligible role in foraging location choice. On the contrary, food availability, elevation or silt content may have played a decisive role in the choice of the foraging sites at the initial site selection stage. For instance, expected prey availability may have led to the collective selection of a location by a flock or may have influenced location choices by leading animals whose choices were copied by followers (Valone & Templeton 2002; Danchin et al. 2004; Dall et al. 2005; Conradt & Roper 2005).

When animals respond to both the presence of conspecifics and environmental cues, the interpretation of the regression coefficients becomes more complicated because the indirect effects generated by social aggregation must be taken into account. That is, food availability initially attracts animals (direct effect) which attract conspecifics and so on (indirect effects). The total effect consists of the sum of the direct and indirect effects. We estimated not only the direct effects, but also, by means of the spatial multiplier, the total effects of exogenous predictors and found that the total effects tend to exceed substantially the direct effects. Note that typically only direct effects are considered in habitat selection models (Campomizzi et al. 2008).

The coefficients of social aggregation and of the exogenous variables change in opposite directions by resolution. Particularly, whereas the relative contributions of social aggregation increase with resolution, the contributions of the exogenous variables decrease, and vice versa. This suggests that there may be some scale-dependent replacement between social aggregation and the exogenous predictors. Indeed, for models made up of the same exogenous environmental predictors, the total impacts were more constant than the regression coefficients for the three resolutions.

The findings in this paper are in line with field studies in that the level of spatial dependence was highest for dunlins and red knots, followed by curlews, oystercatchers, bar-tailed godwits and grey plovers. These results are supported by other field observations of

spatial distributions of these species (Goss-Custard 1970; Piersma 1985).

We have found that the amount of variance explained by environmental predictors is low. This is not because all sampled mudflats are similar in resource availability. Previous studies (Kraan et al. 2009a, b, 2010) have shown that there is substantial variation in food availability across sites. Hence, the small impacts of food availability found here cannot be ascribed to the fact that food is abundant and more or less uniformly distributed so that location selection is irrelevant. An additional conclusion is that the tendency of shorebirds to aggregate leads to suitable habitat remaining unoccupied.

Instantaneous habitat selection decisions of shorebirds are influenced by relatively predictable factors such as food availability and by more unpredictable factors such as wind-related exposure of mudflat or the presence of mobile predators (see e.g. summary in Piersma, 2012). Assessment of the quality of the entire resource landscape by shorebirds will thus always be imperfect and will lead to suboptimal decisions. In a population of nonsocial foragers this kind of imperfect knowledge leads to many small 'mistakes' and thus an overall strong effect of the predictable exogenous predictors. In a population of social individuals, an entire group will make a mistake that increases population-level mismatch with the predictable exogenous variables. It follows that the classical ideal free distribution theory in combination with generalized functional response models is of limited use for predicting the distribution of social foragers. The approach applied here in the context of social foraging of shorebirds should be applicable to a wide range of behavioural phenomena that are driven by a combination of exogenous factors and interindividual pull and push tendencies, that is, situations in which the feedbacks make it difficult to disentangle and estimate the strengths of the different forces.

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